

THE OCEAN AS A NET HETEROTROPHIC SYSTEM:  
IMPLICATIONS FROM THE CARBON  
BIOGEOCHEMICAL CYCLE

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Abstract. The global ocean apparently consumes more organic carbon than it produces. The excess heterotrophy probably occurs in the nearshore zone. This nearshore heterotrophy has significant implications with respect to processes such as organic matter transport from the nearshore zone to the adjacent open ocean, nutrient limitation of primary production, and the role of the coastal zone as a short-term sink for anthropogenic CO<sub>2</sub>.

TABLE 1. Estimates of Primary Production and Respiration in the Global Ocean.

Reference	p	r <sup>a</sup>	p-r	p/r
Reiners [1973]	4167	5417	-1250	0.769
Likens et al. [1973]	3750	3784 <sup>b</sup>	-34	0.991
Olson et al. [1985]	2500	2497	+3	1.001

Fluxes in units of 10<sup>12</sup> mol C yr<sup>-1</sup>.

<sup>a</sup>"Respiration" includes the terms respiration, decay, and decomposition, as used in the various models.

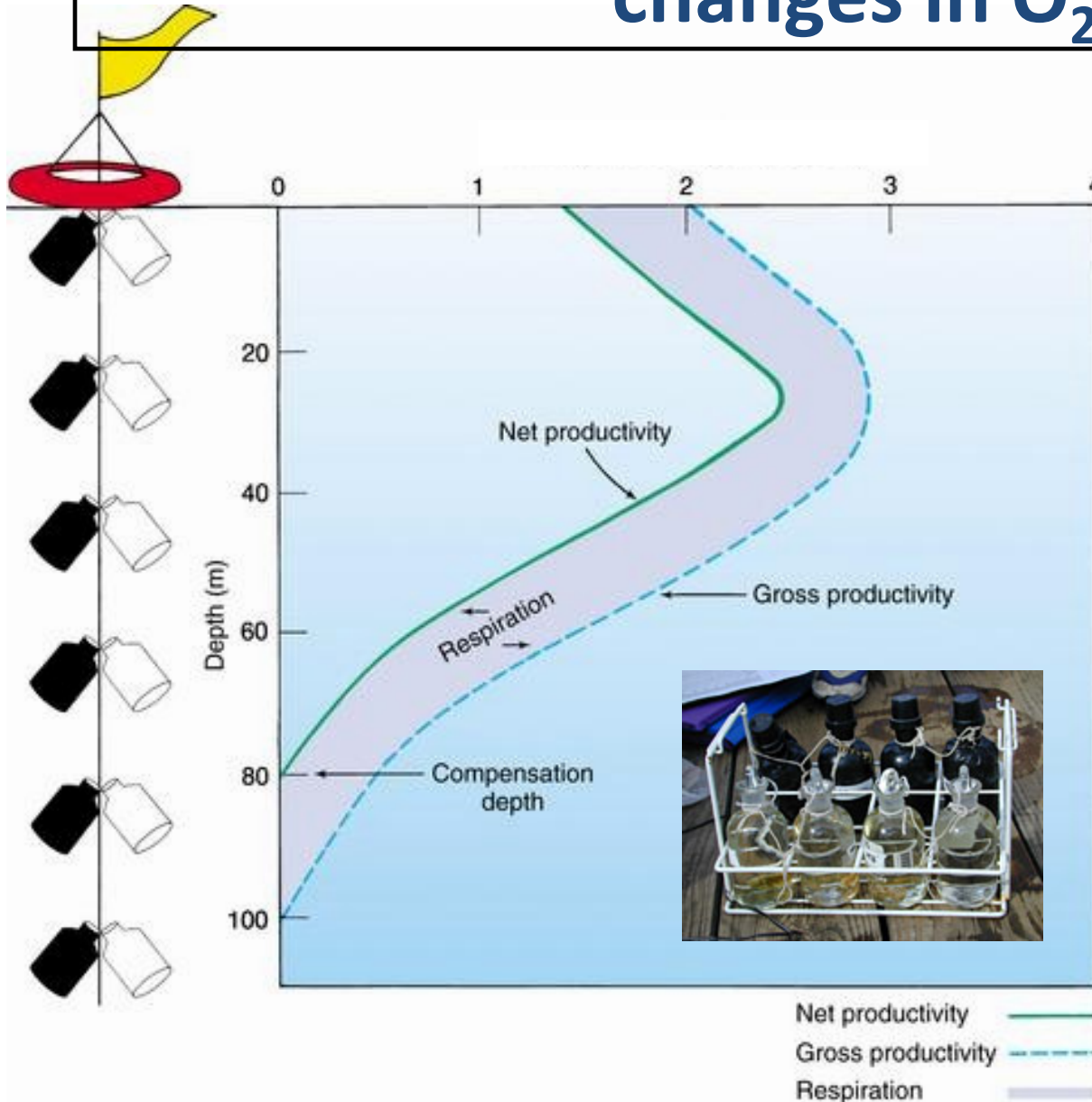
<sup>b</sup>Average of a range of estimates: 3767-3800.

**Net Community Production (NCP): Gross primary production less all autotrophic and heterotrophic losses due to respiration (R<sub>A+H</sub>).**

$$\text{NCP} = P_G - R_{A+H}$$

- The ocean "appears" to be net heterotrophic, i.e. NCP is negative...
- Apparent global shortfall of 500 x 10<sup>15</sup> moles C, or ~10% of oceanic production
- The ocean should soon have no free oxygen

# Productivity and respiration by changes in O<sub>2</sub>



- Measures changes in oxygen concentrations in light and dark bottles following incubation
- Light bottle = net community production (photosynthesis and community respiration).
- Dark bottle: community respiration.
- Light + Dark = Gross primary production

$$GPP = \Delta O_2 (\text{light}) - \Delta O_2 (\text{dark})$$

# Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems

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PLANKTONIC bacteria are a fundamental component of the organic carbon cycle in aquatic systems<sup>1</sup>. Organic carbon consumption by planktonic bacteria is the sum of bacterial production (BP) and bacterial respiration (BR). It is now estimated that 30–60% of phytoplankton production (the amount of inorganic carbon fixed by phytoplankton photosynthesis, corrected for phytoplankton respiration) in marine and freshwater systems is processed by bacteria<sup>1–3</sup>. These estimates of carbon flow through bacteria are conservative, however, because losses due to bacterial respiration are seldom directly measured<sup>4,5</sup>. We report here that bacterial respiration is generally high, and tends to exceed phytoplankton net production in unproductive systems (less than 70 to 120 µg carbon per litre per day). A large proportion of the world's aquatic systems have phytoplankton productivities below this value<sup>6</sup>. Bacterial growth efficiency (BGE) is the result of BP and BR [BGE = BP/(BR + BP)]. Comparisons of our models of bacterial respiration with published models of bacterial secondary production<sup>1,7</sup> show that bacterial growth efficiency must range from less than 10% to 25% in most freshwater and marine systems, well below the values commonly assumed in many current ecological models<sup>1,2,8,9</sup>. The imbalance between

# The CO<sub>2</sub> Balance of Unproductive Aquatic Ecosystems

Carlos M. Duarte\* and Susana Agusti

Community respiration ( $R$ ) rates are scaled as the two-thirds power of the gross primary production ( $P$ ) rates of aquatic ecosystems, indicating that the role of aquatic biota as carbon dioxide sources or sinks depends on its productivity. Unproductive aquatic ecosystems support a disproportionately higher respiration rate than that of productive aquatic ecosystems, tend to be heterotrophic ( $R > P$ ), and act as carbon dioxide sources. The average  $P$  required for aquatic ecosystems to become autotrophic ( $P > R$ ) is over an order of magnitude greater for marshes than for the open sea. Although four-fifths of the upper ocean is expected to be net heterotrophic, this carbon demand can be balanced by the excess production over the remaining one-fifth of the ocean.

Aquatic ecosystems cover 70% of Earth's surface ( $I$ ) and contribute 45% of the global primary production (2). Yet, the role of their biota in the global CO<sub>2</sub> budget remains a subject of debate (3–5). Many freshwater ecosystems act as CO<sub>2</sub> sources (6); in contrast, oceanic ecosystems are assumed to act as CO<sub>2</sub> sinks (7, 8). This assumption has been challenged by calculations suggesting that the coastal ocean may be net heterotrophic (9) and by the finding that bacterial metabolism exceeds phytoplankton production in unproductive waters (10), which

make up >30% of the ocean. These conclusions are based on indirect calculations and controversial assumptions (3). Here, we compare the gross primary production ( $P$ ) and respiration ( $R$ ) rates of aquatic communities to elucidate whether the biota of aquatic ecosystems acts as net CO<sub>2</sub> sources ( $R > P$ ) or sinks ( $R < P$ ). We compiled data obtained over the past five decades from studies in which oxygen evolution was used as a surrogate for carbon fluxes (11).

Community metabolism varied by over four orders of magnitude across aquatic ecosystems (Table 1). Marshes tended to be more productive than other aquatic ecosystems, whereas open sea communities showed the lowest production and respiration rates (Table 1). The

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# The balance of plankton respiration and photosynthesis in the open oceans

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carbon balance. There is no evidence of the large regional imbalances observed previously<sup>2</sup>. I conclude that the form of data analysis is critical.

## TECHNICAL COMMENTS

### Regional Carbon Imbalances in the Oceans

Recent studies (1, 2) have suggested that respiration exceeds photosynthetic oxygen production in large areas of the oceans. If correct, the conclusion has profound implications for our understanding of the oceanic carbon cycle. C. M. Duarte and S. Agustí conclude that four fifths of the ocean are net

is the gross primary production rate. This equation is an unsatisfactory model when extrapolating across ecosystems of widely different productivities because the term "a" is not constant, but dependent on the scale of local photosynthesis [table 1 in the report (2)]. The  $P = a + bP_g$  relationship attempts to fit a sin

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# Respiration in the open ocean

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A key question when trying to understand the global carbon cycle is whether the oceans are net sources or sinks of carbon. This will depend on the production of organic matter relative to the decomposition due to biological respiration. Estimates of respiration are available for the top layers, the mesopelagic layer, and the abyssal waters and sediments of various ocean regions. Although the total open ocean respiration is uncertain, it is probably substantially greater than most current estimates of particulate organic matter production. Nevertheless, whether the biota act as a net source or sink of carbon remains an open question.

## brief communications

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### COMMUNICATIONS ARISING

#### Global carbon cycle

## Metabolic balance of the open sea

The rise of oxygenic photosynthesis nearly three billion years ago led to the accumulation of free oxygen and to the subsequent diversification of life on Earth; today, nearly half of all oxygen production derives from the photosynthetic activities of marine phytoplankton<sup>1</sup>. The conclusion that the open sea — and therefore much of our planet's surface — is in a net heterotrophic metabolic state<sup>2–4</sup> is enigmatic and is a first-order question in the global carbon cycle, as discussed by del Giorgio and Duarte<sup>5</sup>. Our

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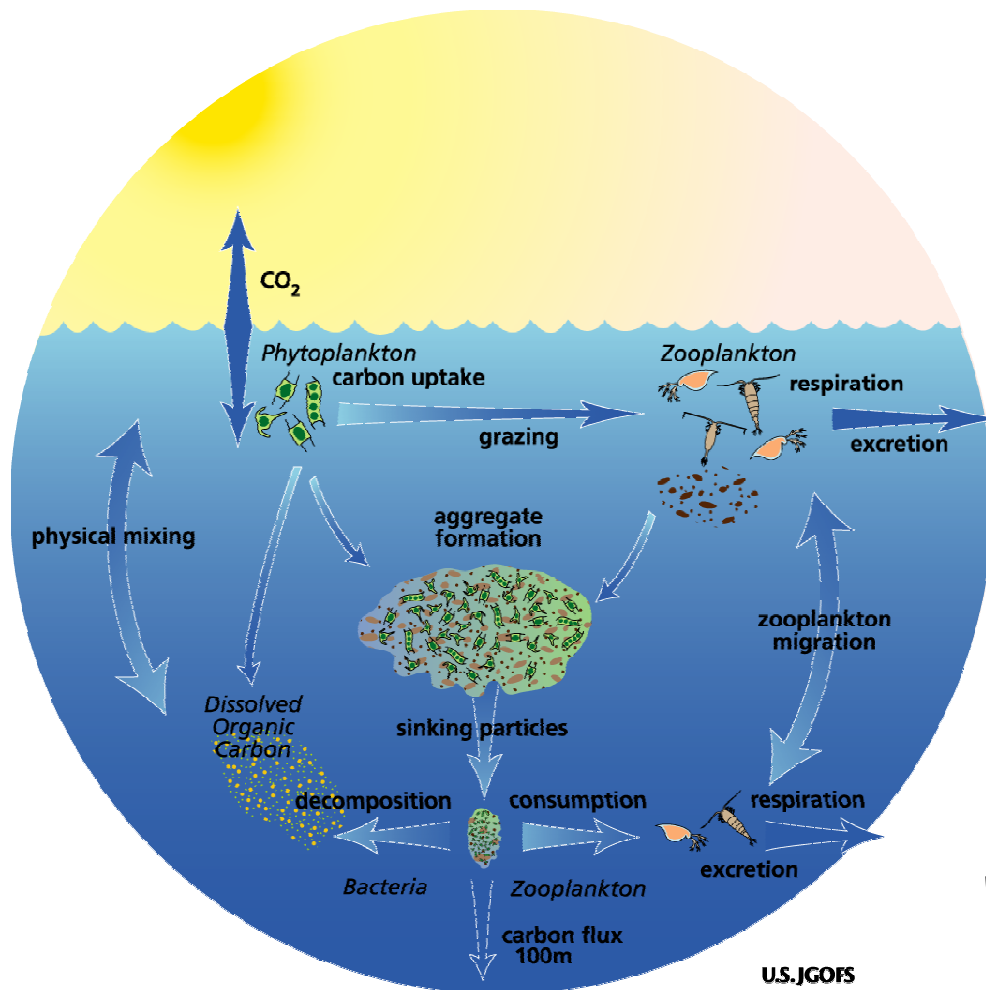
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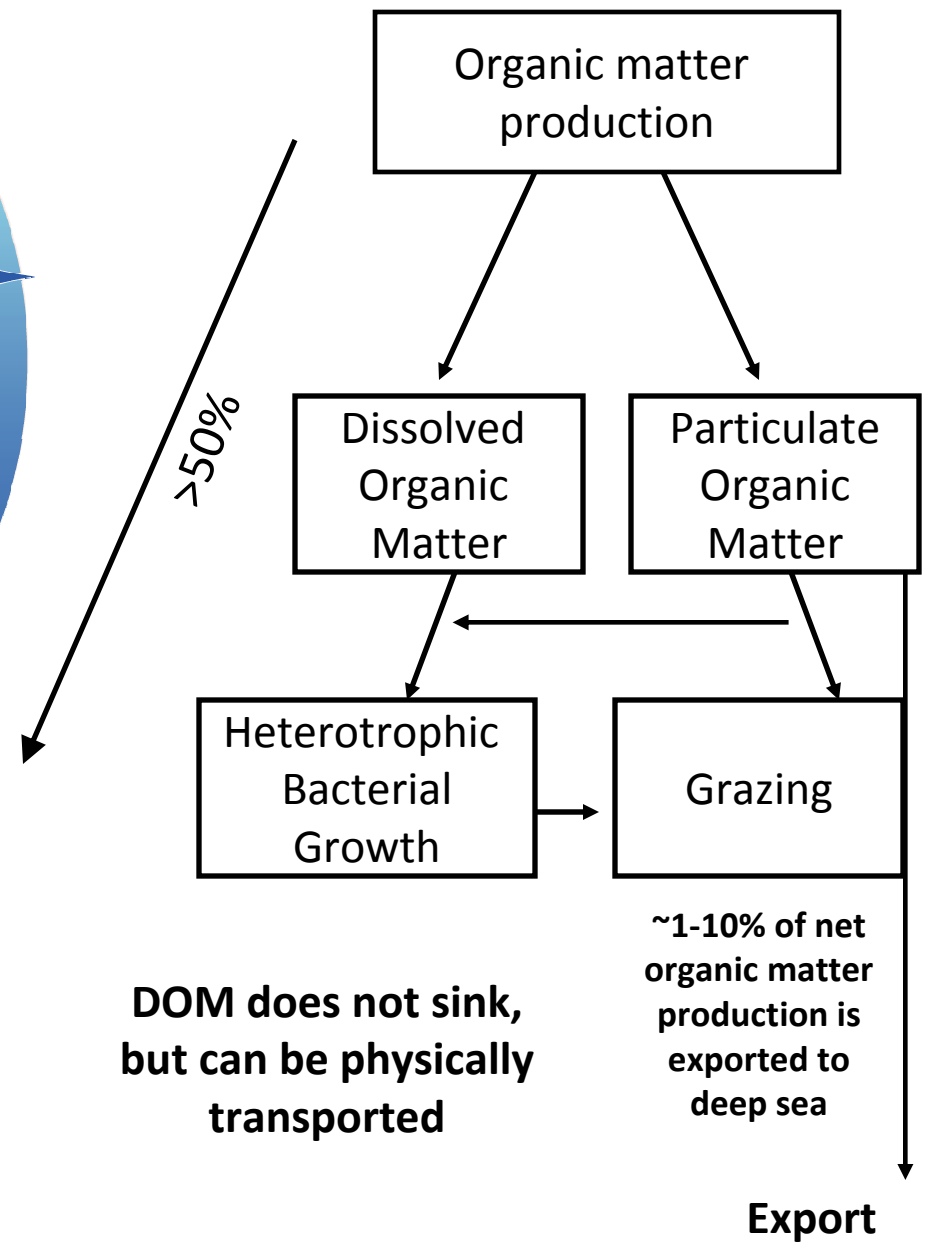
<sup>‡</sup> *School of Oceanography, University of Washington, Seattle, Washington 98195, USA*

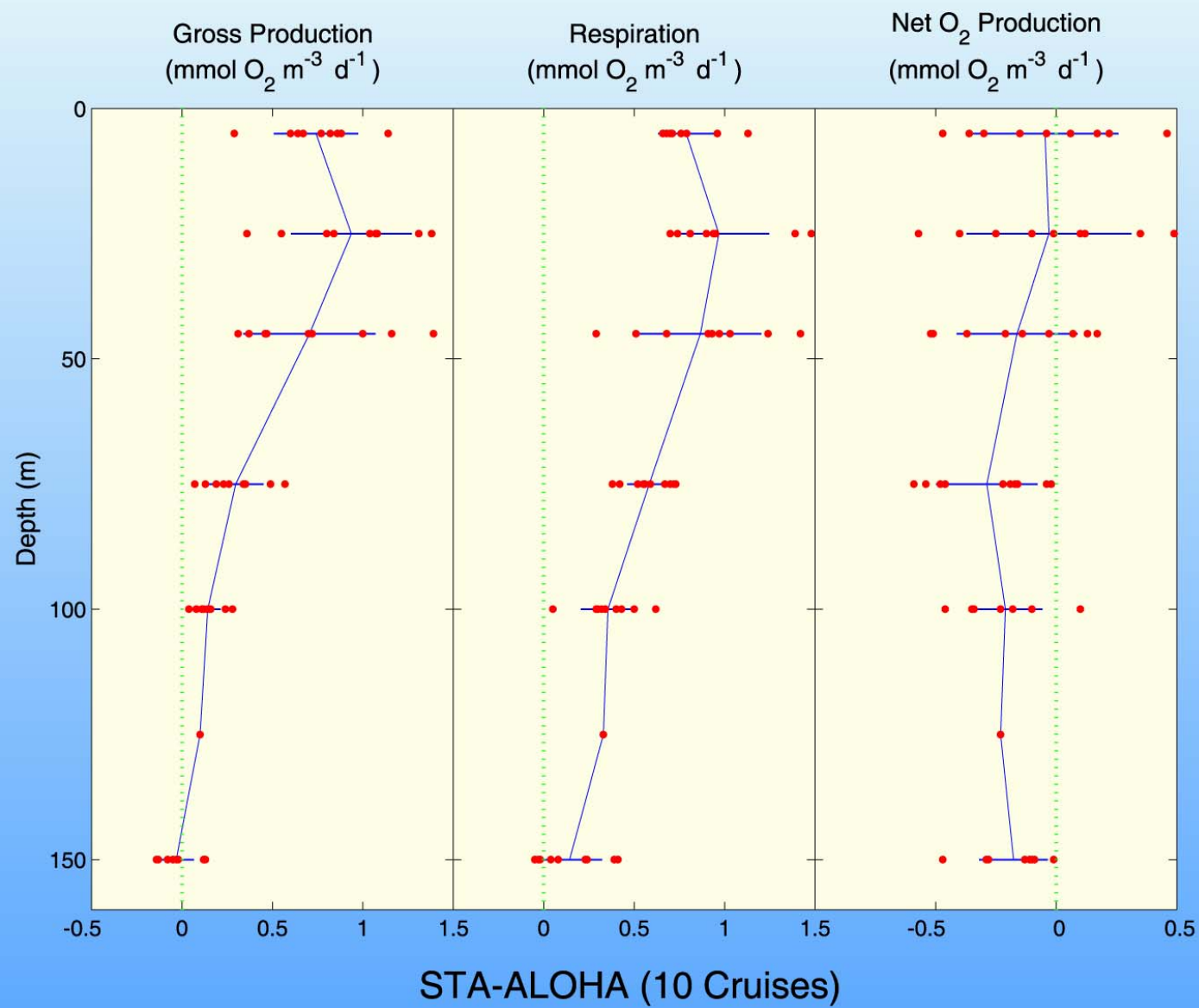
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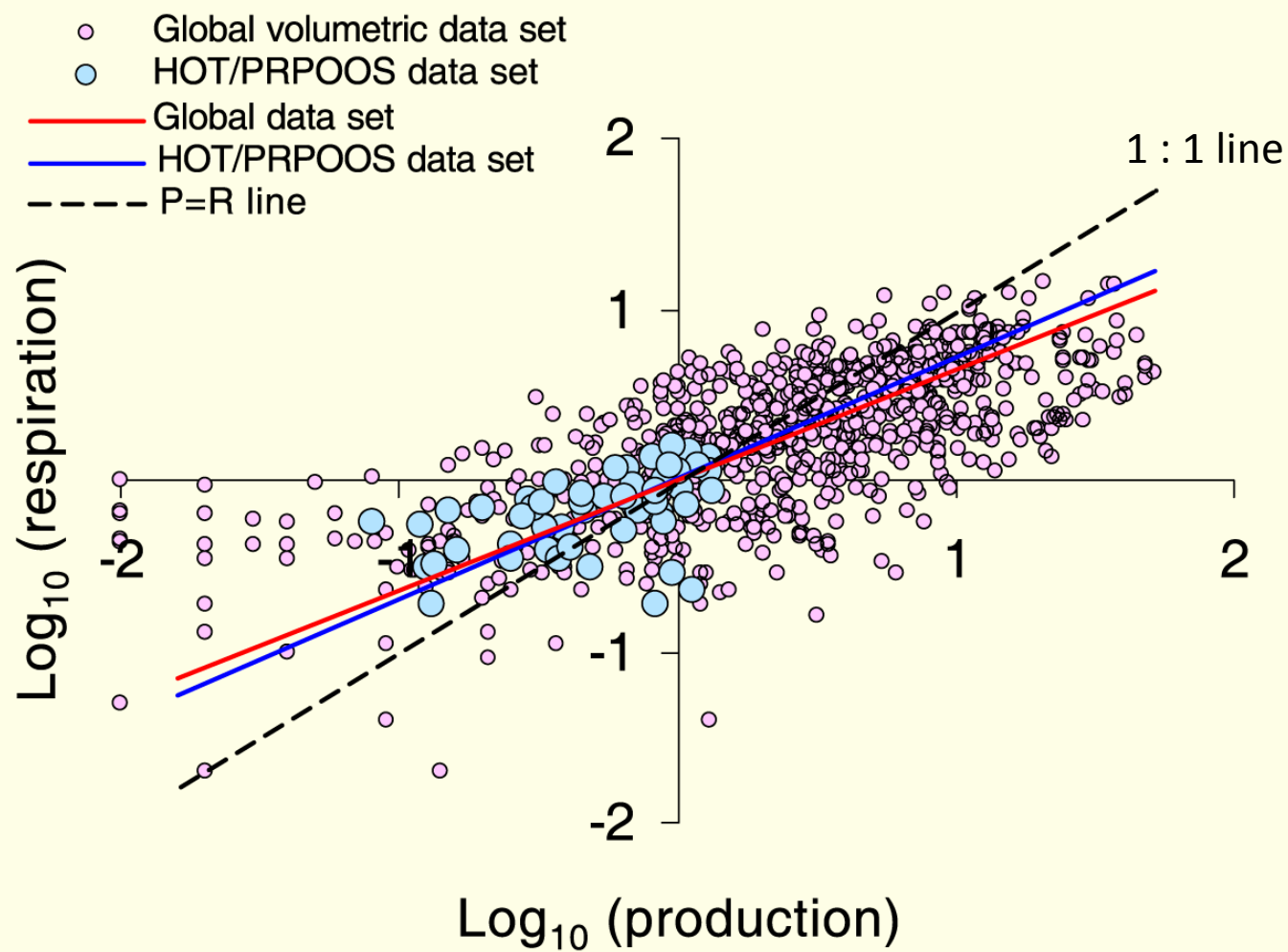
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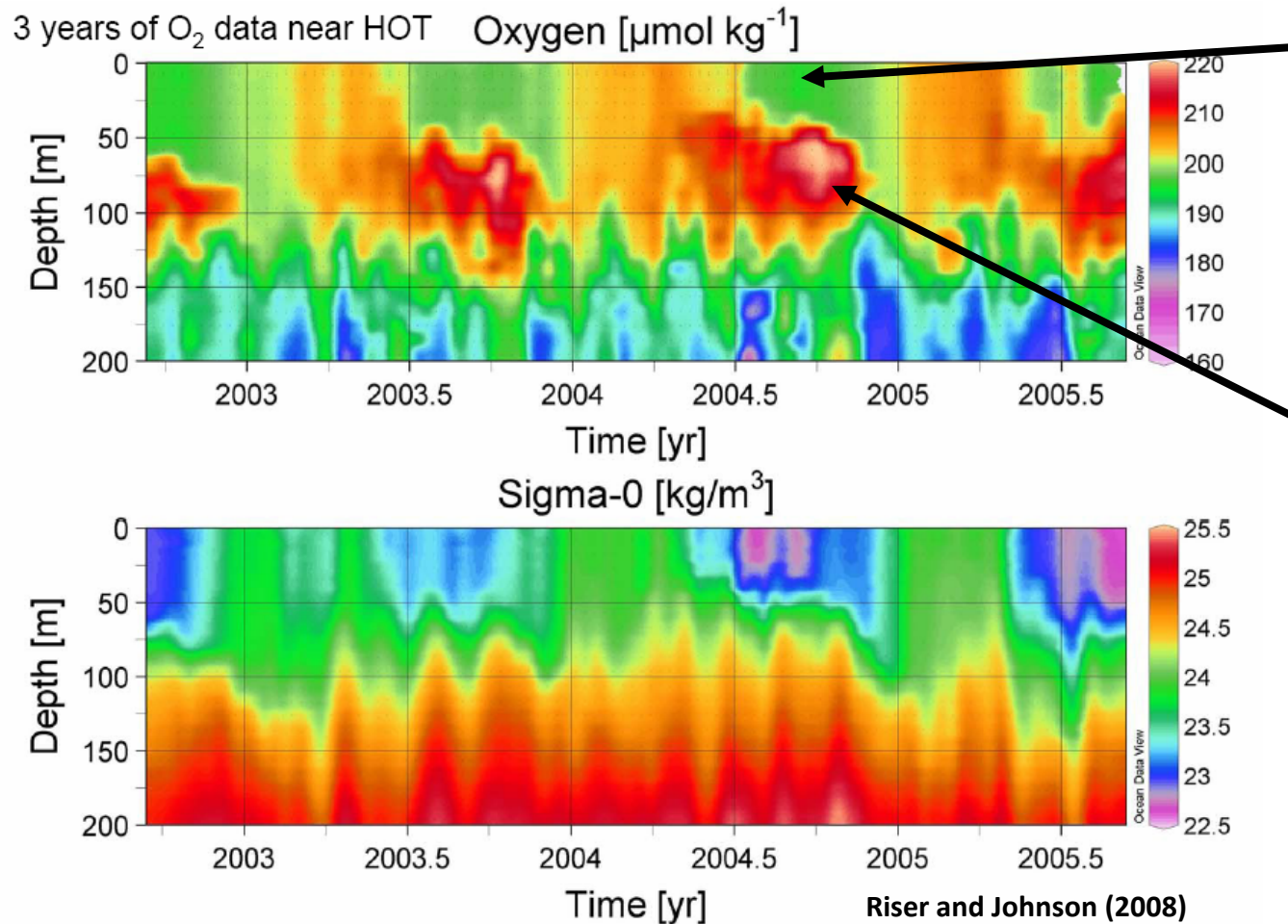
**Organic matter export from the upper ocean implies that production exceeds respiration; otherwise there would be no organic matter to export.**







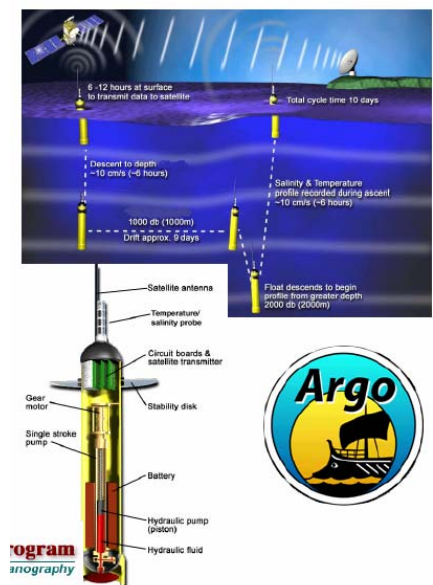


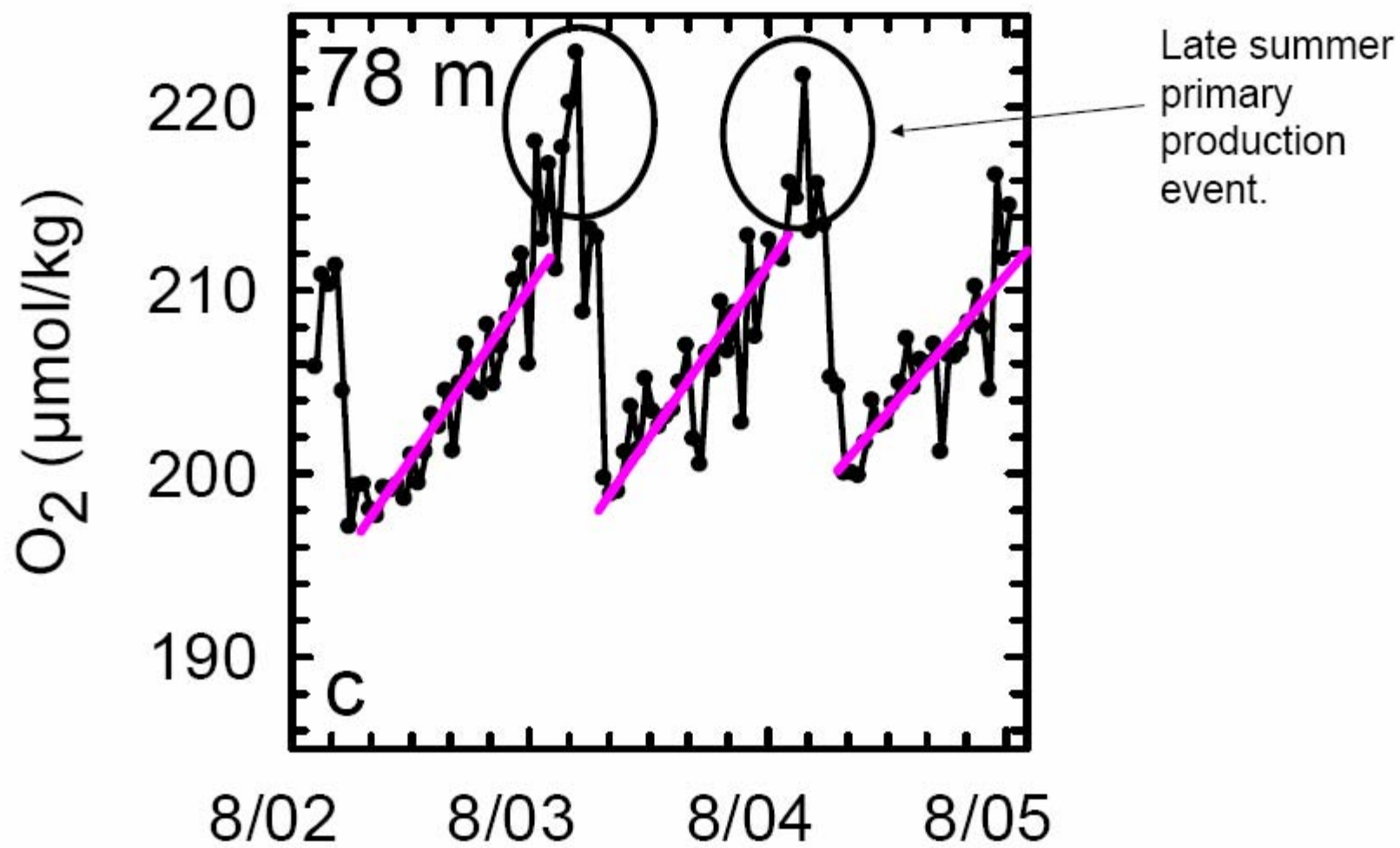


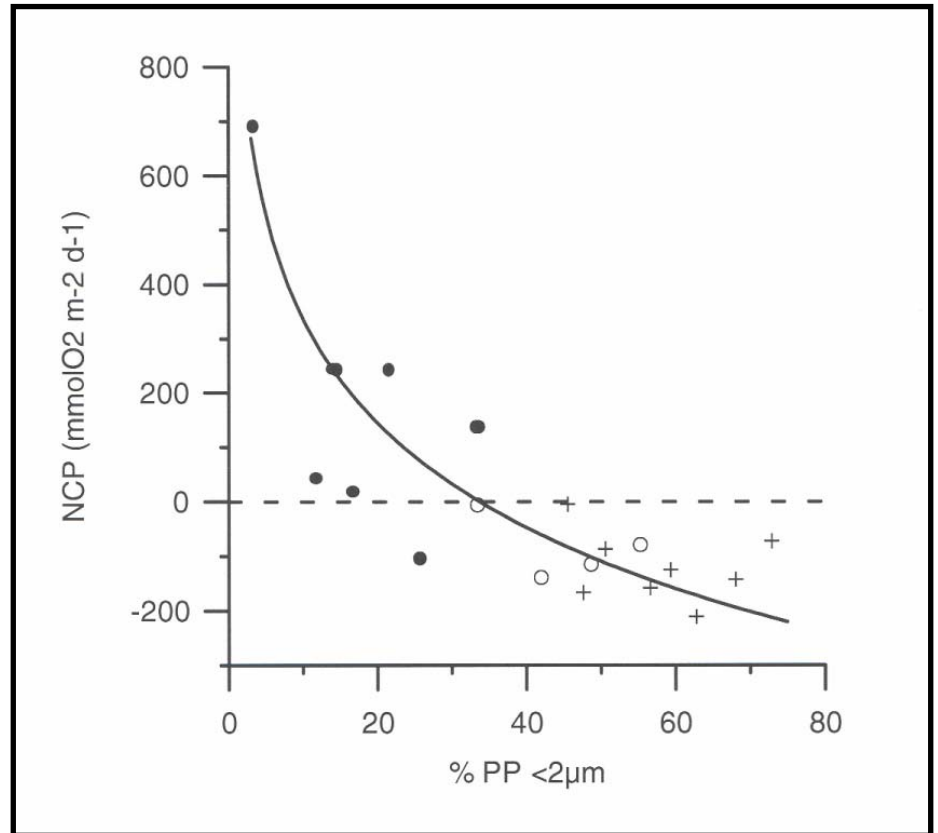
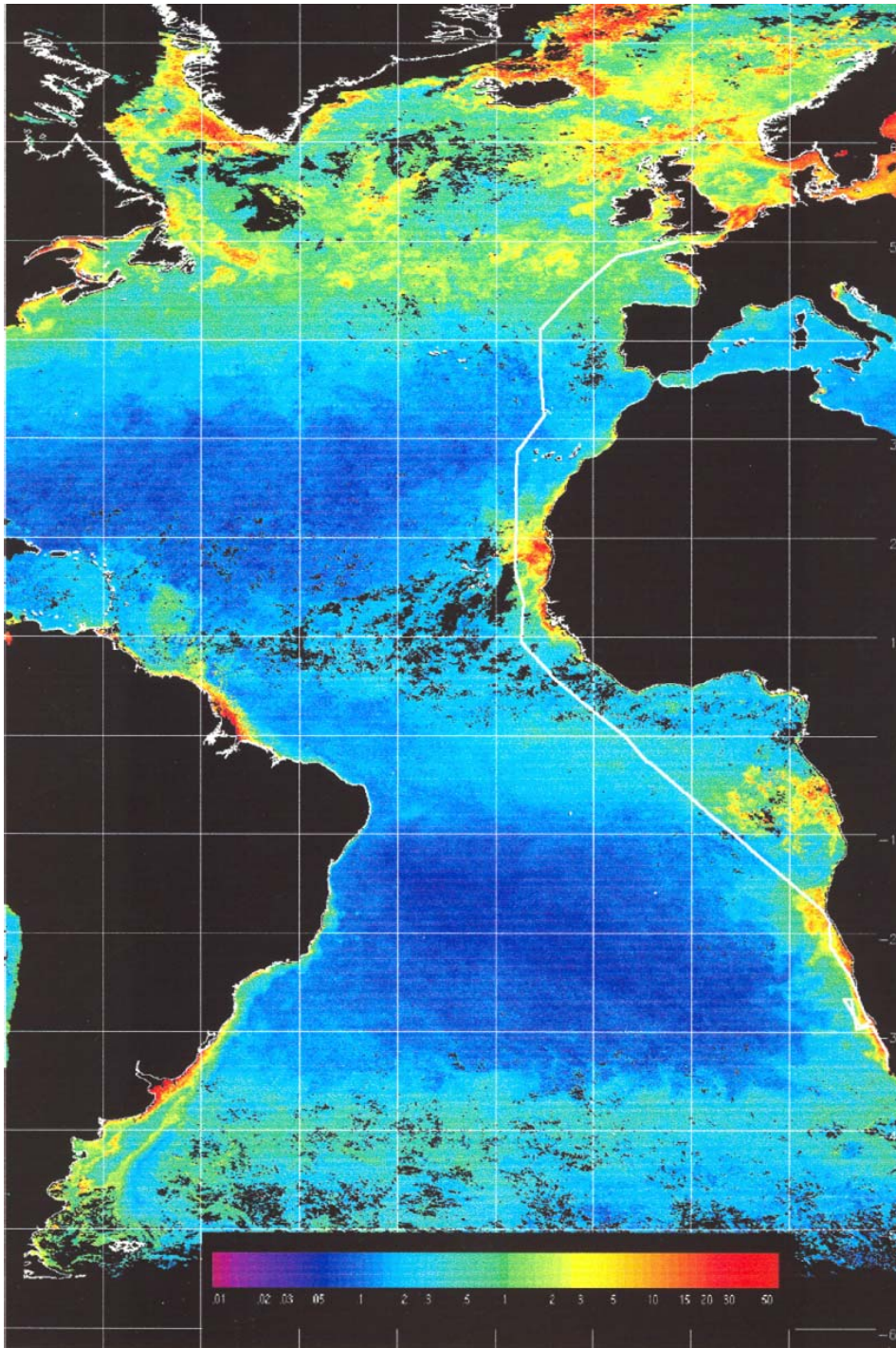
Mixed layer O<sub>2</sub> is in equilibrium with the atmosphere

Rate of subsurface O<sub>2</sub> accumulation provides information on NCP

But remember this study?  
Net autotrophic not heterotrophic...



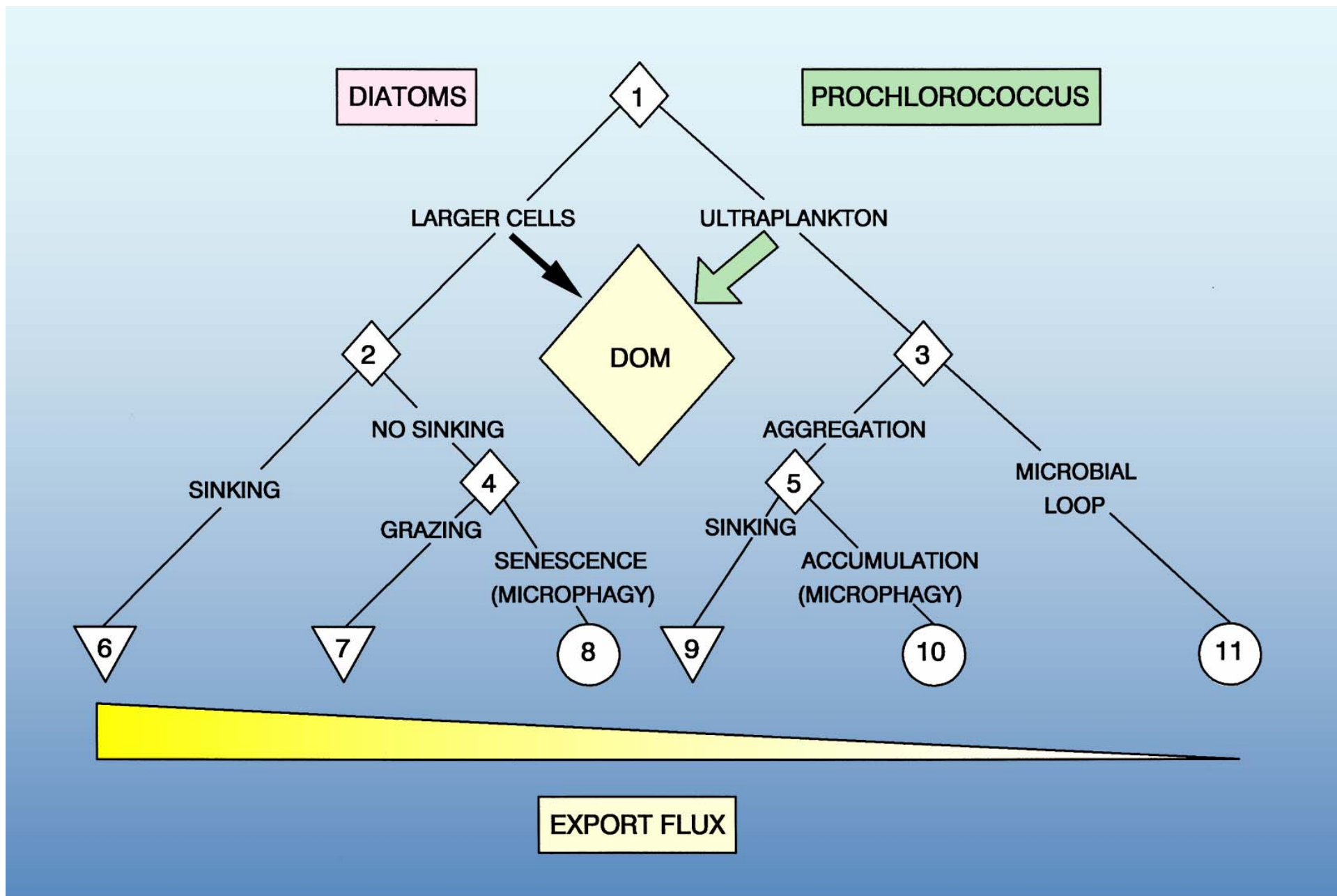




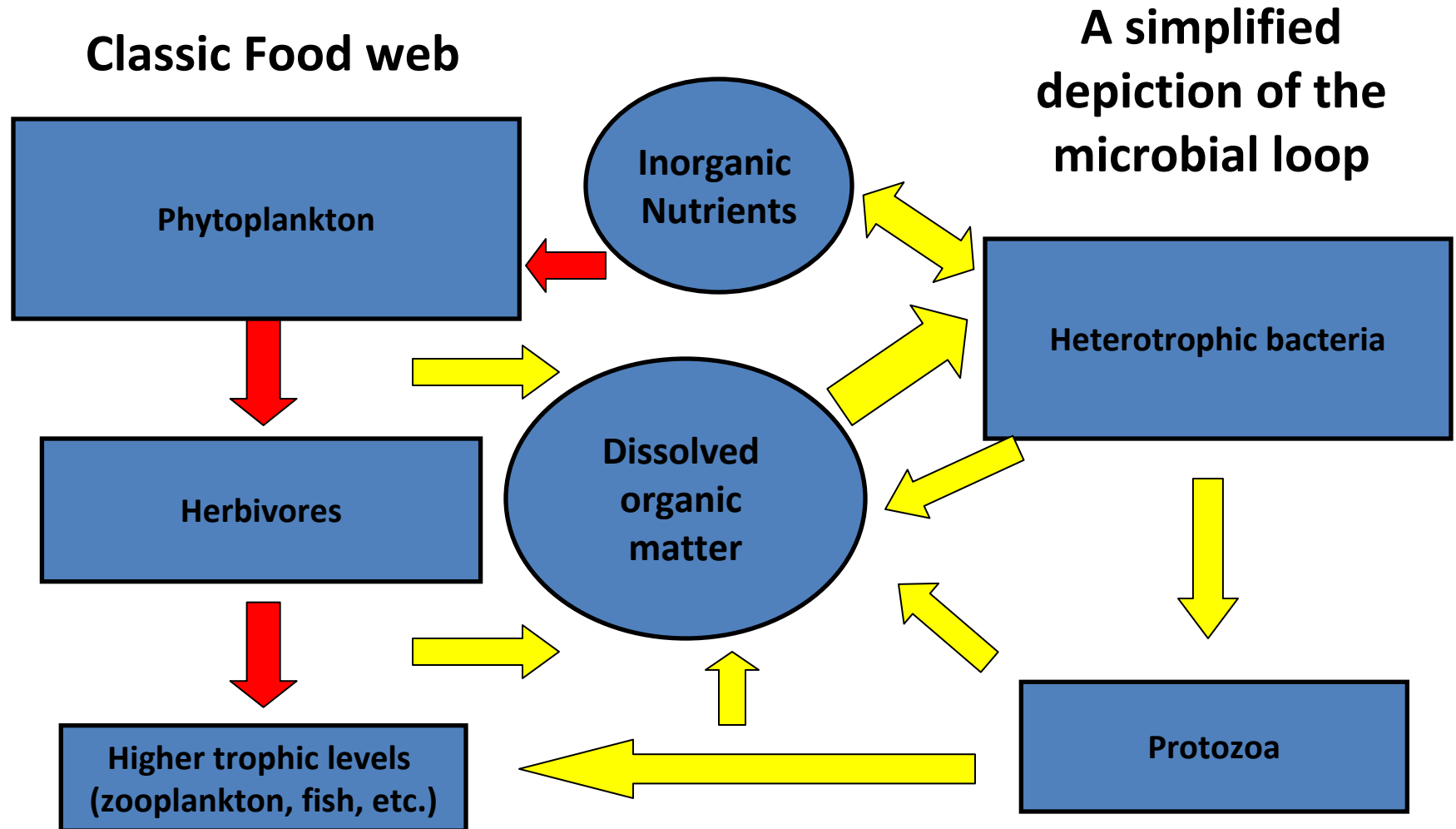
*Serret et al. (2001)*

- Where does primary production go?
  - Export
  - Bacteria
  - Grazing
  - Dissolved organic matter





# The Microbial Loop



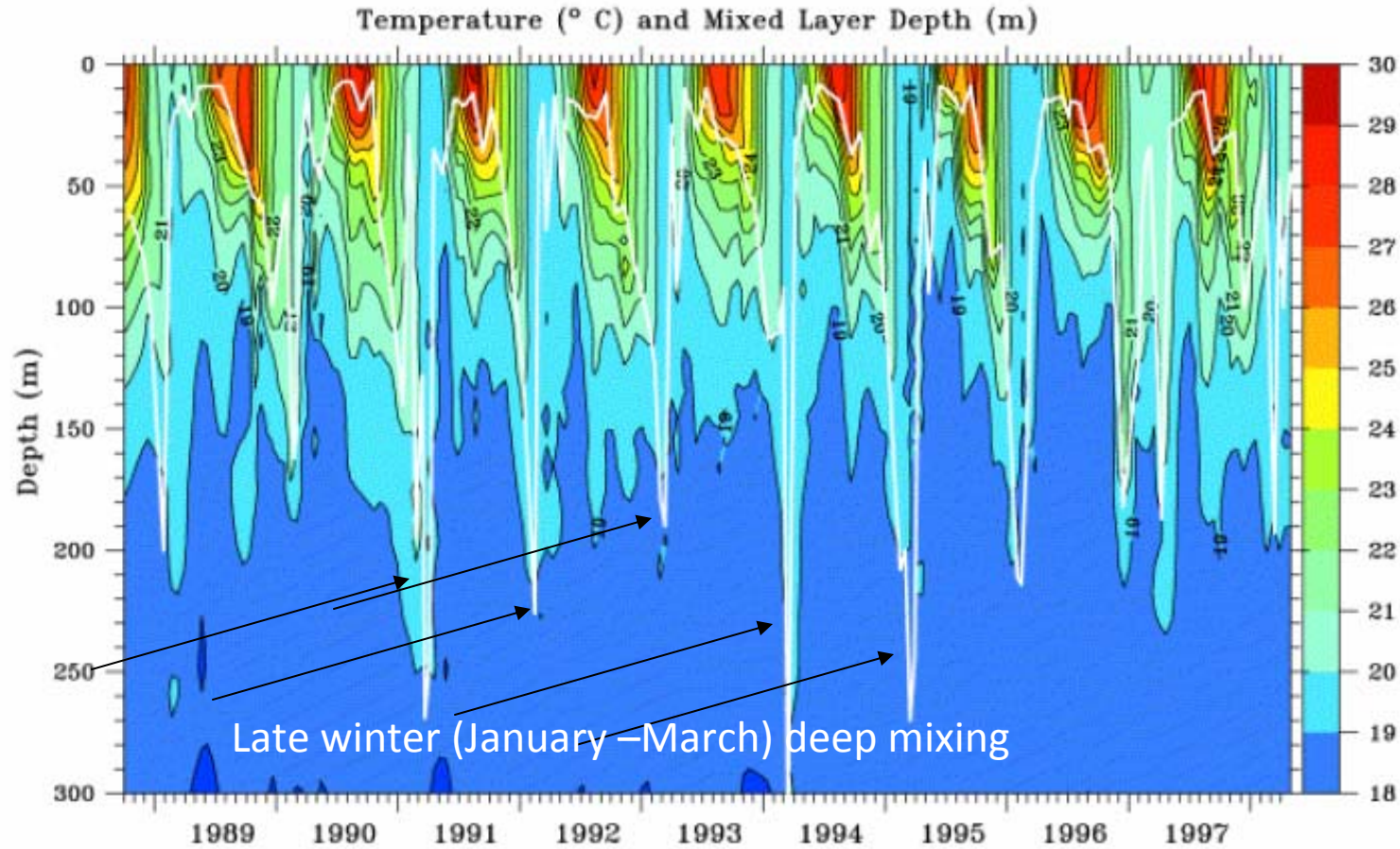
# **What other components of the biological pump are important?**

- The majority of organic material in the ocean is in the dissolved phase (operationally defined as  $<0.7 \mu\text{m}$  or  $0.2 \mu\text{m}$ )

# Why dissolved organics matter

- Dissolved organic matter constitutes the largest global reservoir of fixed carbon  $\sim 700 \times 10^{15}$  g C.
- Oxidation of even 1% of the seawater DOC pool in a 1 year period would exceed annual anthropogenic CO<sub>2</sub> emissions.
- DOC can also serve as an important component of new production.





**Seasonal variations in mixing and temperature in the Sargasso Sea-note winter time deepening of the mixed layer coincides with seasonal cooling.**

# Upper ocean total organic carbon at BATS

Remember DOC = ~98% of the TOC.

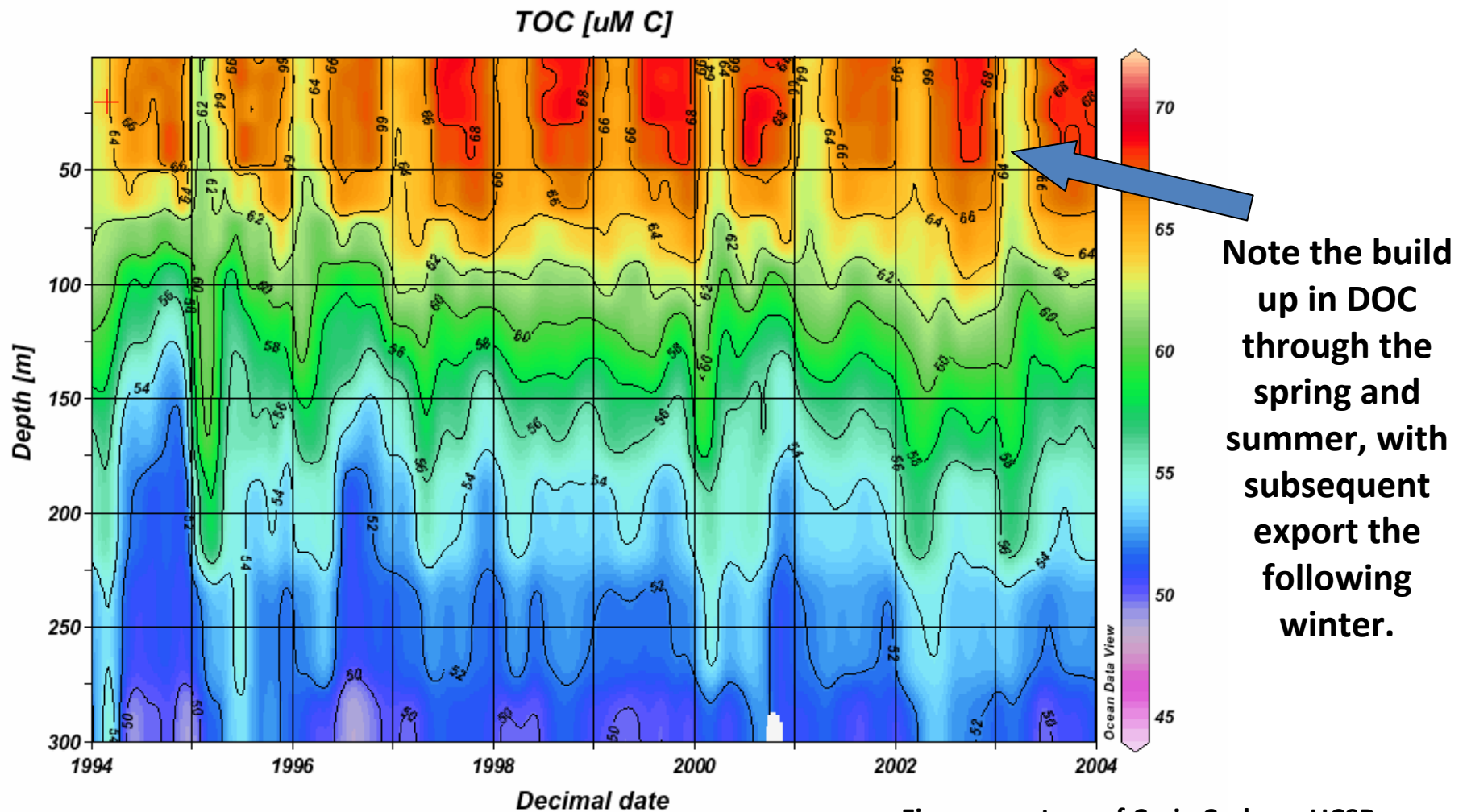


Figure courtesy of Craig Carlson, UCSB

# TOC Profiles at BATS

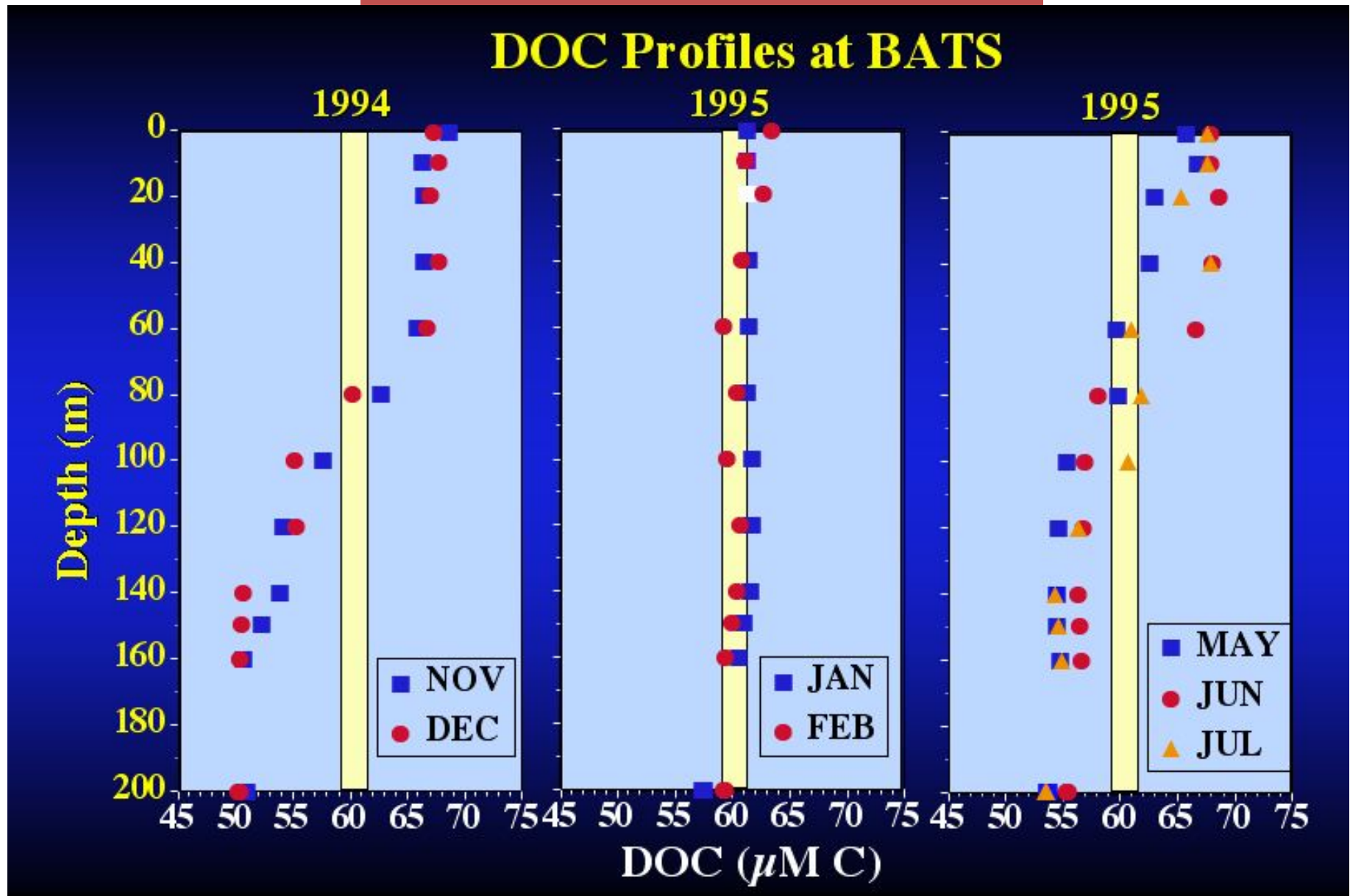
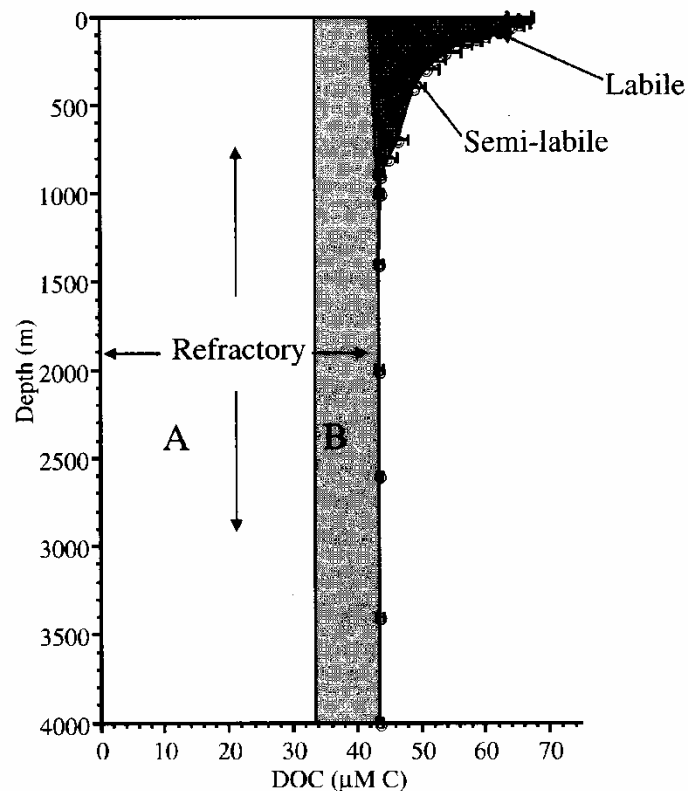


Figure courtesy of Craig Carlson, UCSB



**Figure 5** Conceptual cartoon of the various pools of refractory, semilabile, and labile DOC in the open ocean. This figure is based on the mean profile for all DOC data collected at the Bermuda Atlantic Time-series Study (BATS) site in the Northwestern Sargasso Sea. The magnitude and distribution of the various pools of lability will vary depending on the location of the study site and the degree of thermal stratification of the water column (see Hansell, Chapter 15). The refractory pool is divided into two broad pools based on the deep ocean gradient observed by Hansell and Carlson (1998a). They observed the lowest concentration of DOC ( $34 \mu\text{M C}$ ) in the north Pacific and used this concentration to represent refractory DOC which turns over on time scales of greater than ocean mixing (A, white box). The deep DOC concentrations in excess of the  $34 \mu\text{M C}$  represents the fraction of the biologically refractory pool that turns over on time scales of ocean mixing (i.e., centuries; B, light gray box).

**Typical DOC profile :**  
 elevated in near surface water, decreasing through the thermocline, stable at depth.

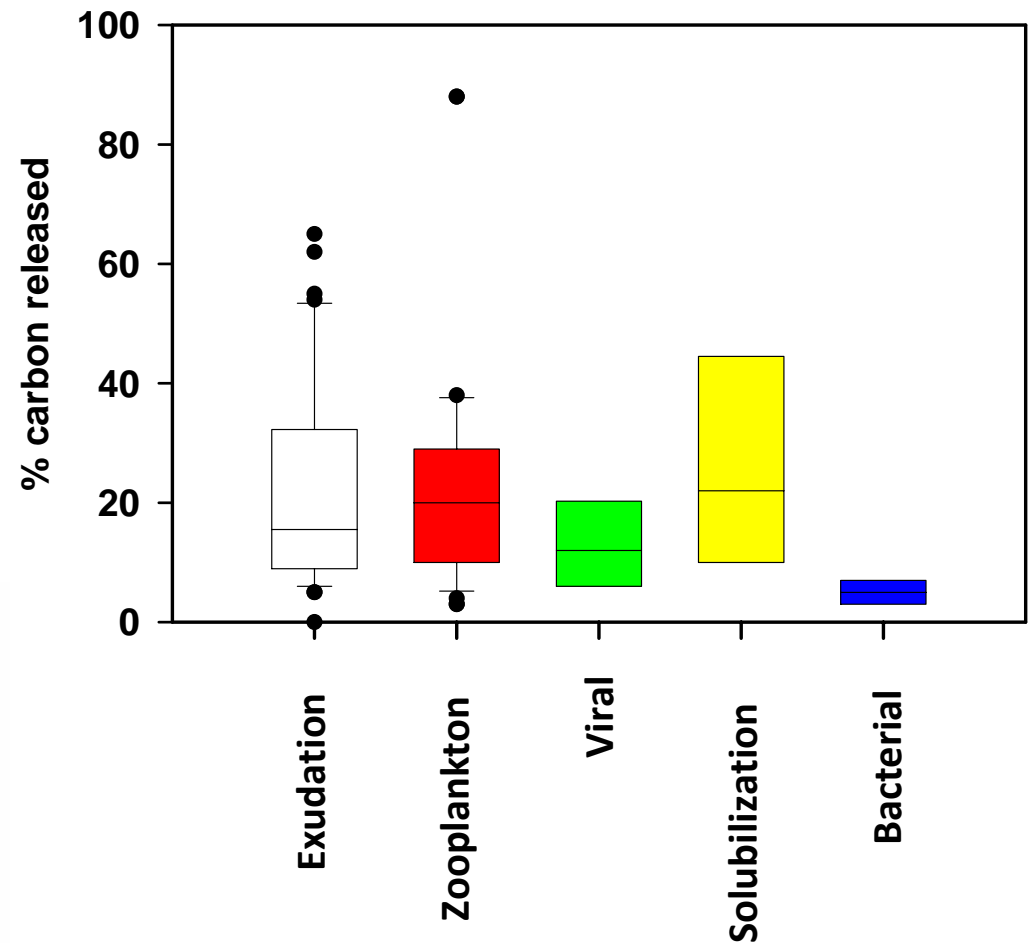
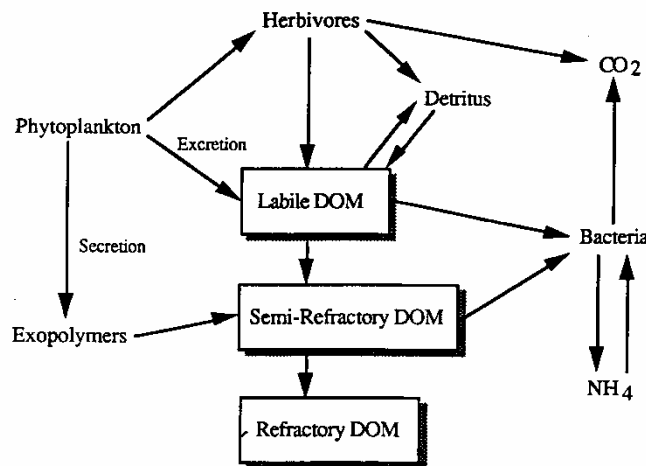
- Labile pools cycle over time scales of hours to days.
- Semi-labile pools persist for weeks to months.
- Refractory material cycles over on time scales ranging from decadal to multi-decadal...perhaps longer...



# Contribution of different sources to marine DOM

## Sources of DOM to ocean ecosystems

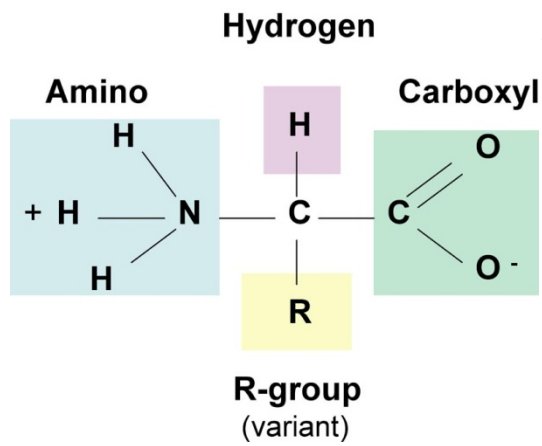
1. Direct algal excretion
2. Zooplankton (sloppy feeding, excretion)
3. Viral lysis
4. Bacterial release
5. Solubilization of POM



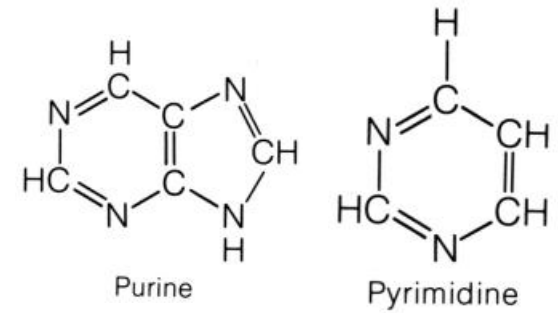
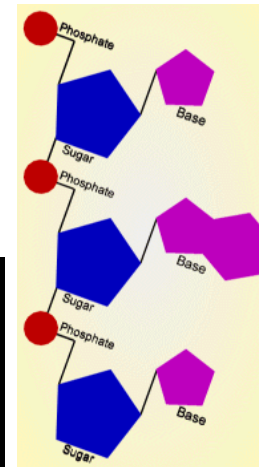
Exudation % <sup>14</sup>C primary production, zooplankton % carbon ingested, solubilization % C released from aggregates, bacterial % release from <sup>14</sup>C labeled organic substrate. Sources: Nagata (2001), Carlson (2002).

Figure 1 Three major pools of dissolved organic matter (DOM) and the processes contributing to them.

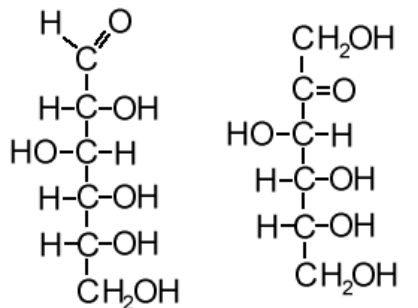
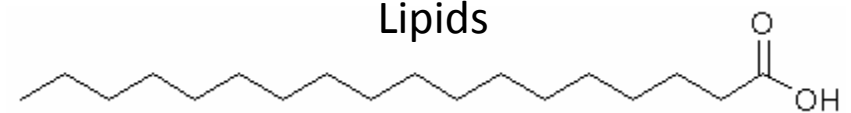
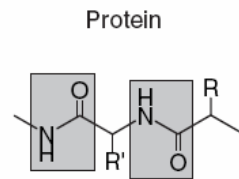
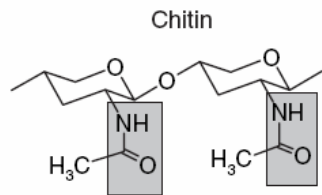
## Amino Acid Structure



**Identified  
DOM  
compound  
classes**

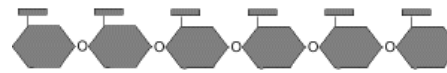


Nucleotides and nucleic acids

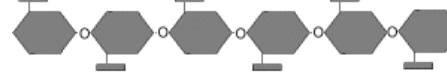


Monosaccharides

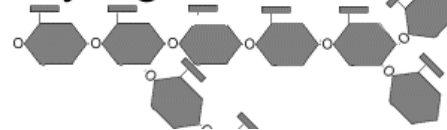
Starch



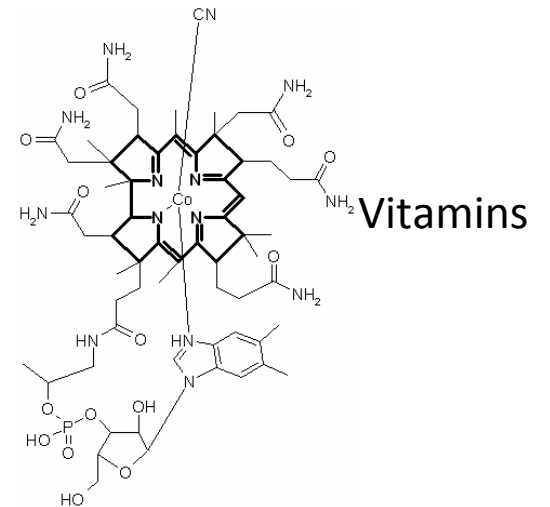
Cellulose



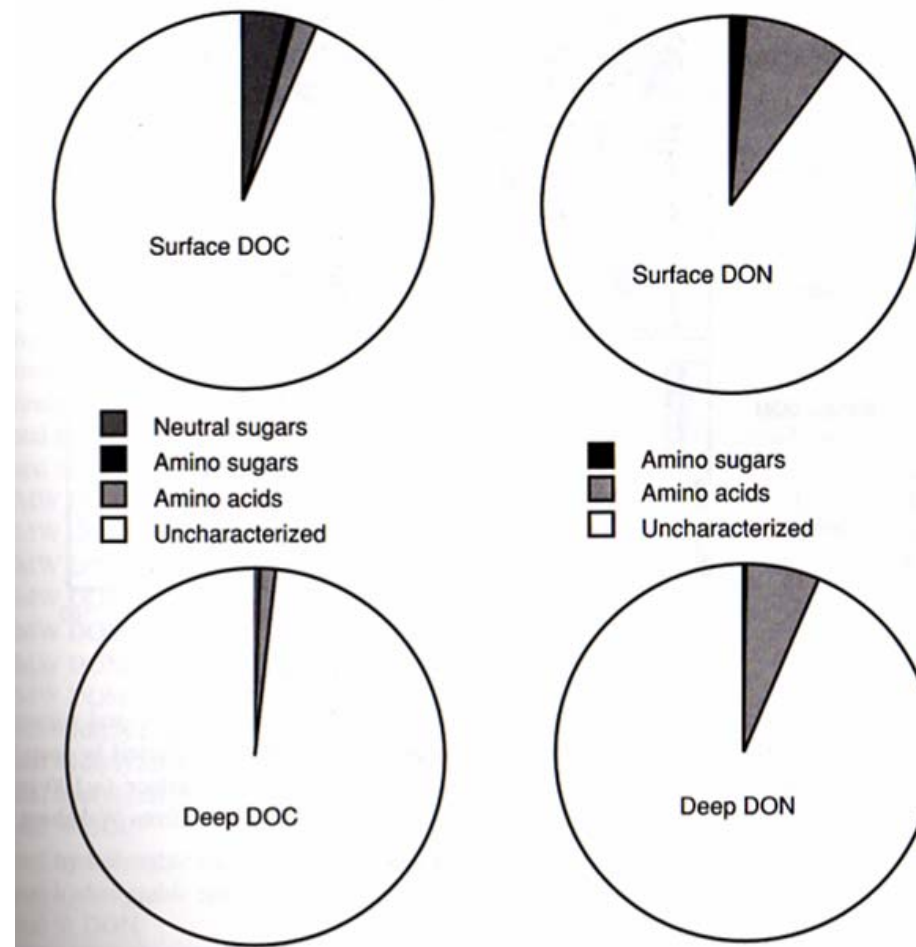
Glycogen



Polysaccharides



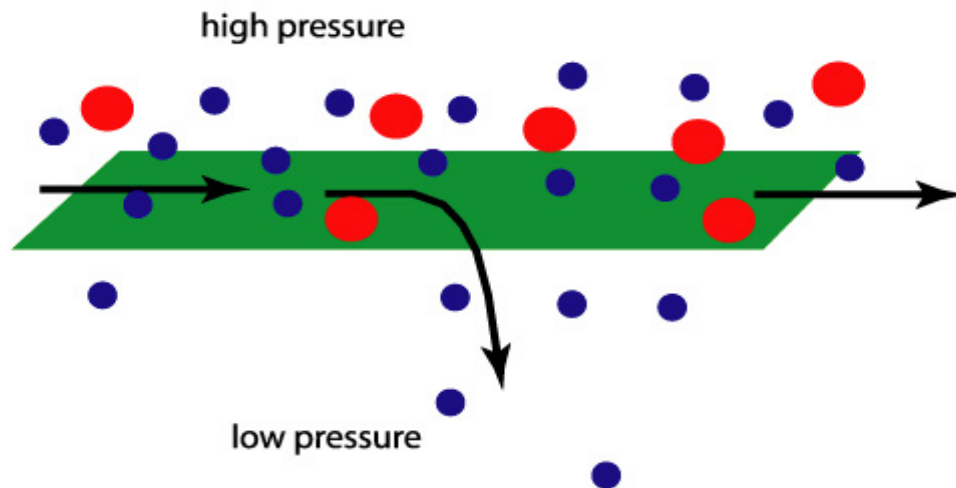
# The vast majority of organic matter in the sea remains chemically uncharacterized



Carbohydrates, neutral sugars, amino acids, and amino sugars make up ~20% of the bulk DOC pool in the upper ocean

# Isolation of DOM by ultrafiltration

## Cross Flow Filtration



Size selective concentration of DOM

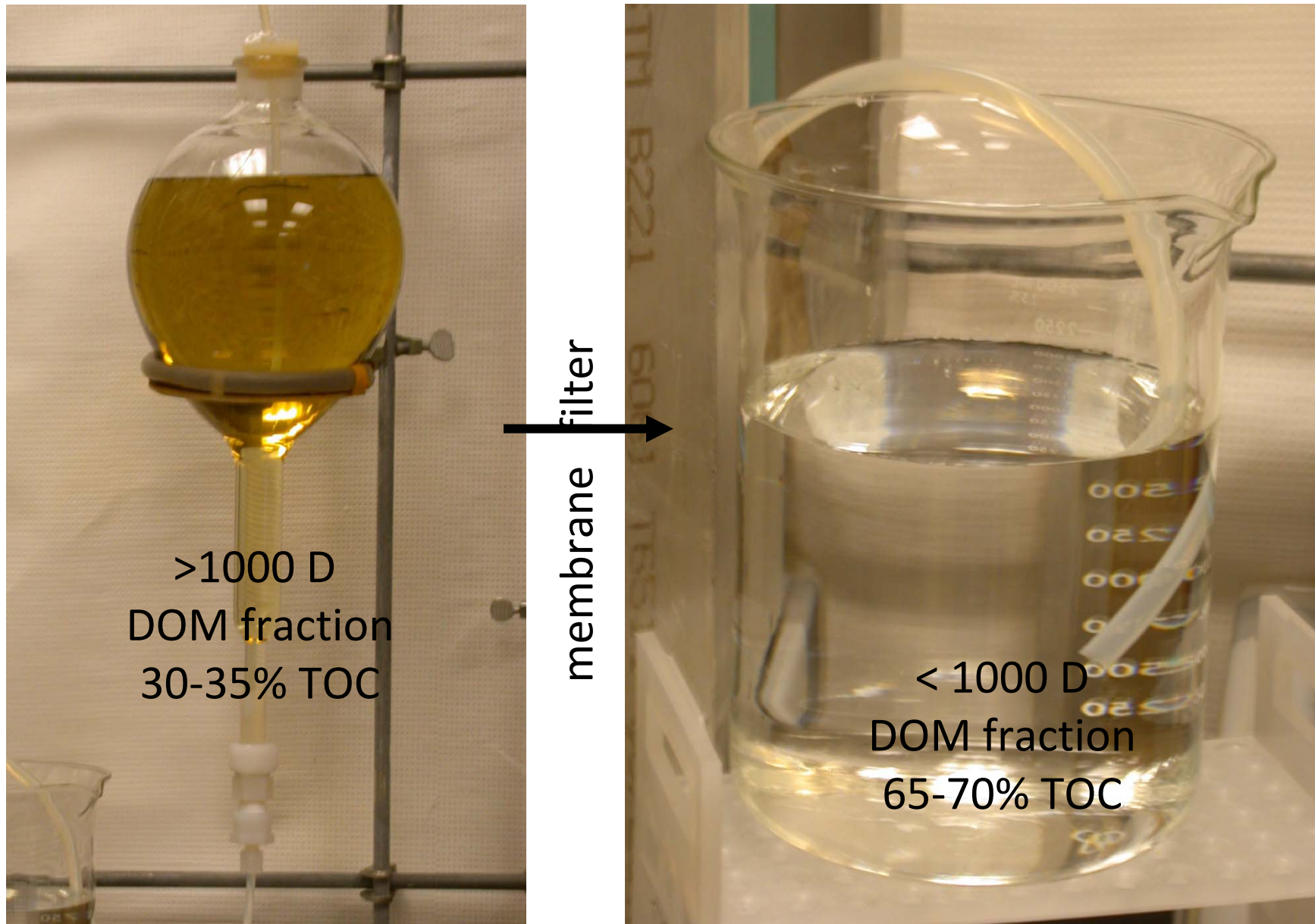
Typically solutes  $> 1\text{nm}$  are concentrated for subsequent analyses

Selects for HMW fraction (about 30-35% TOC)

Some salts collected also



## Ultrafiltration high molecular weight DOM (HMWDOM)



Photos from Dan Repeta



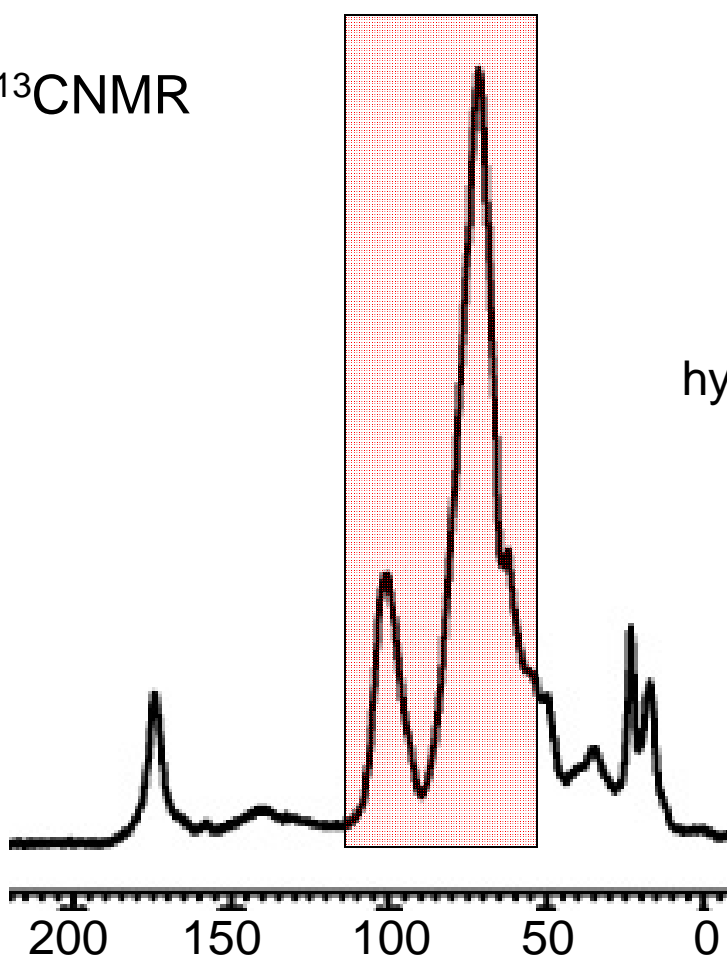
**Final product  
30-35% of total DOC**



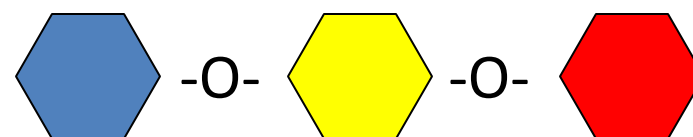
# Spectral and chemical analyses of HMWDOC

Carbohydrate  
50-70% of HMWDOC

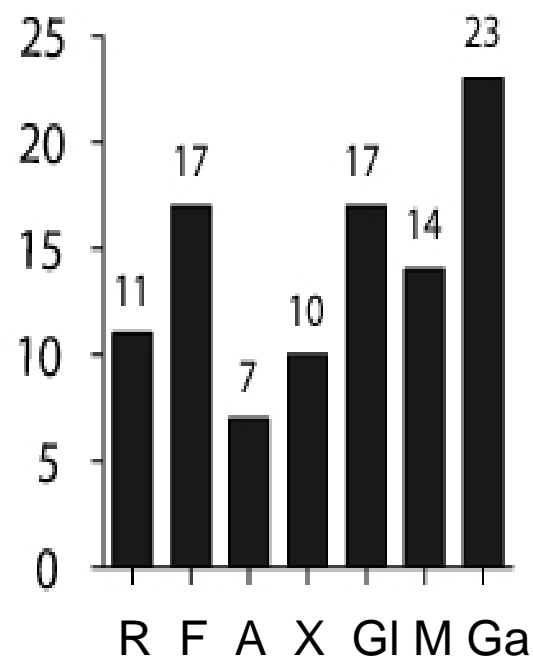
$^{13}\text{C}$ NMR



Acid  
hydrolysis  
→

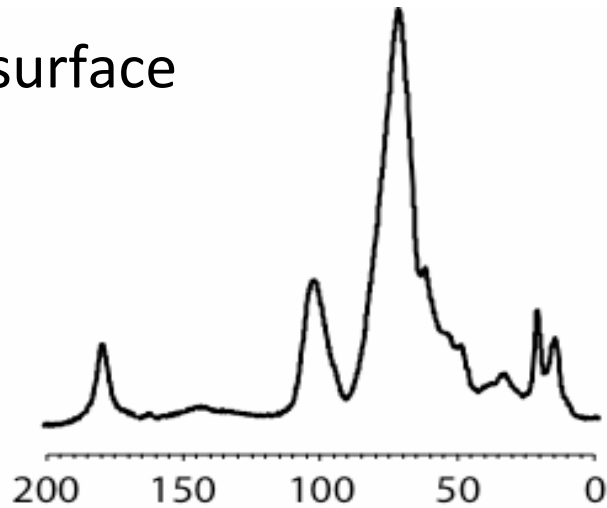


Acid hydrolysis followed by  
Monosaccharide analyses  
yields 7 major neutral sugars  
that represent 5-10% of surface water DOM

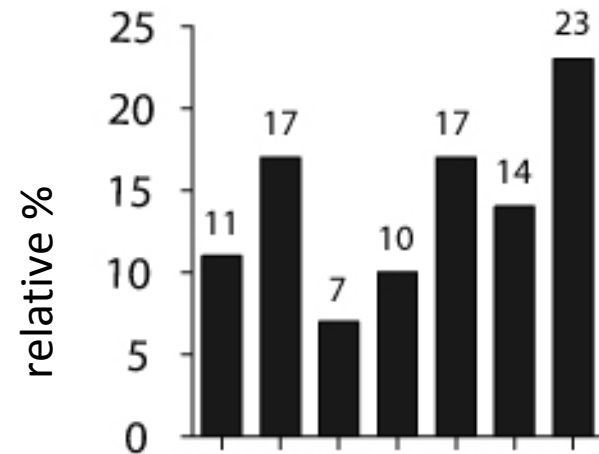


# NMR and carbohydrate analyses of deep sea HMWDOC

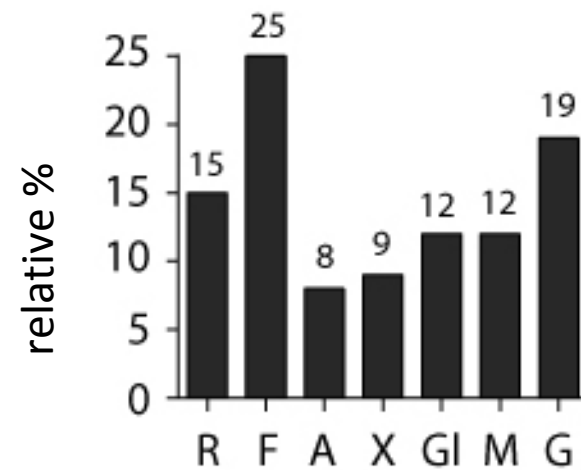
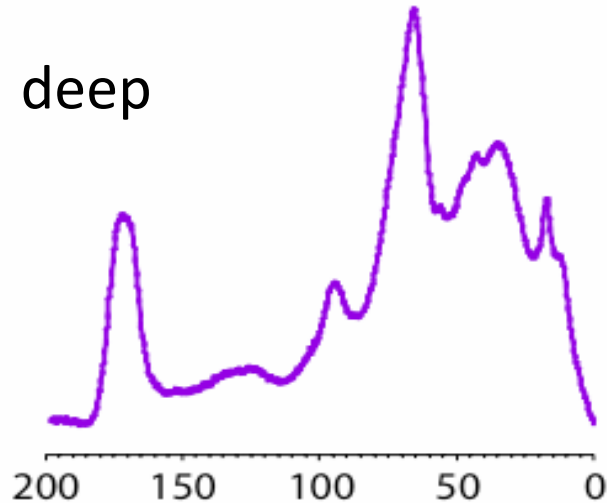
surface

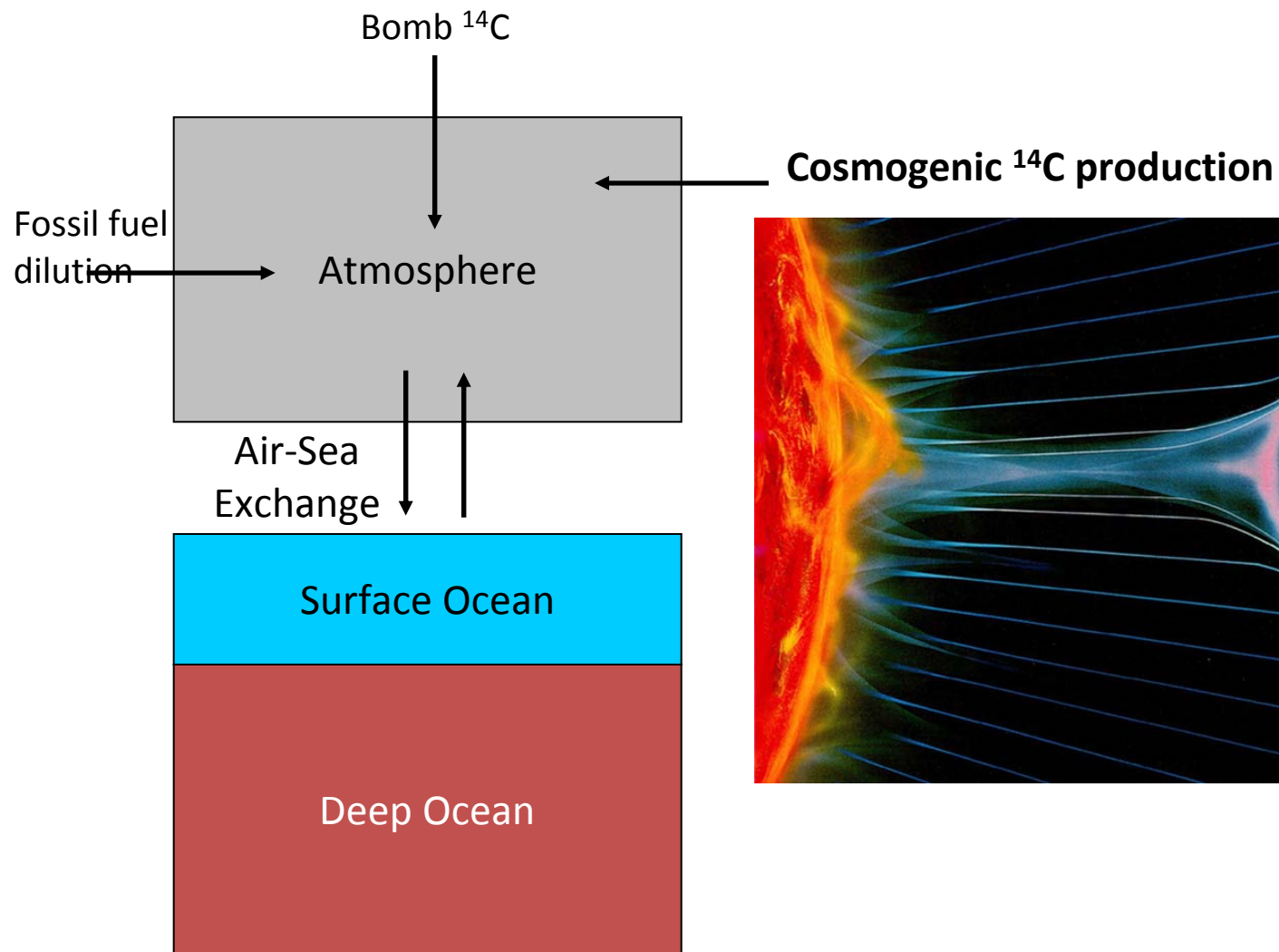


monosaccharide distribution

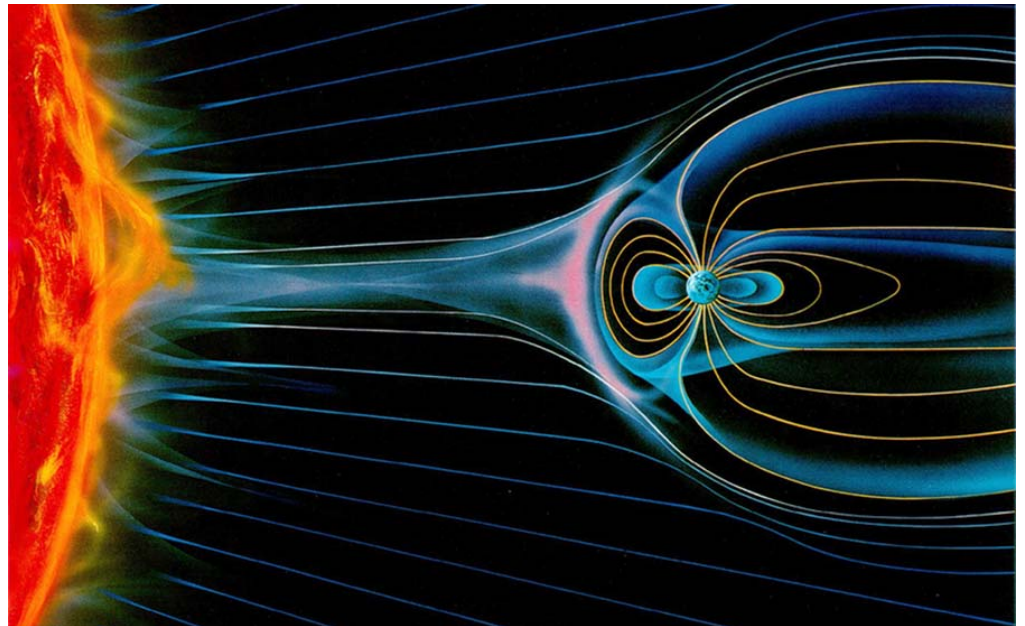


deep





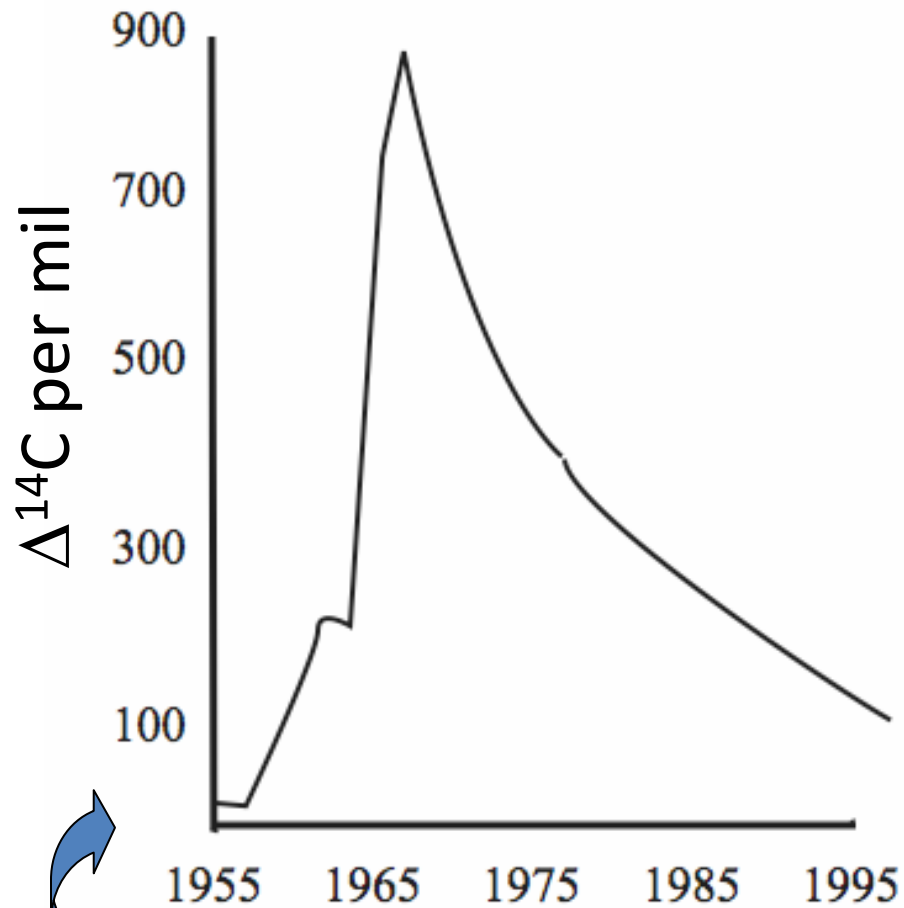
Factors controlling  $^{14}\text{C}$  in  
atmospheric and oceanic  
reservoirs



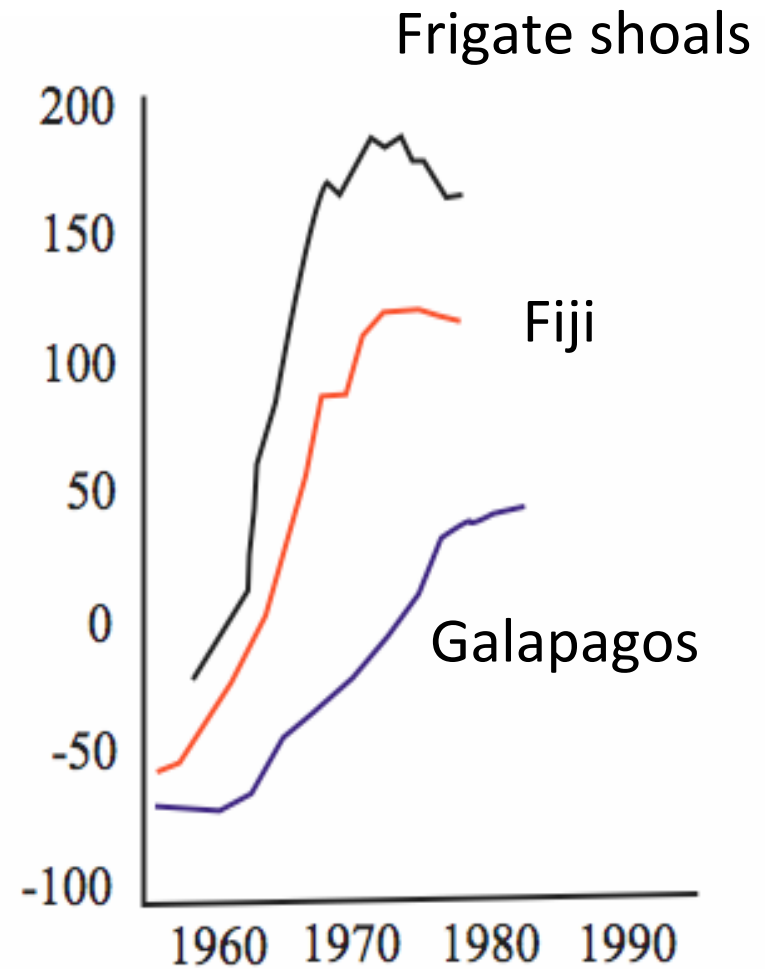
**$^{14}\text{C}$  half-life is 5730 years**



# History of radiocarbon in the Atmosphere and ocean



Prebomb value of -80 per mil



# DOC cycling via DO<sup>14</sup>C

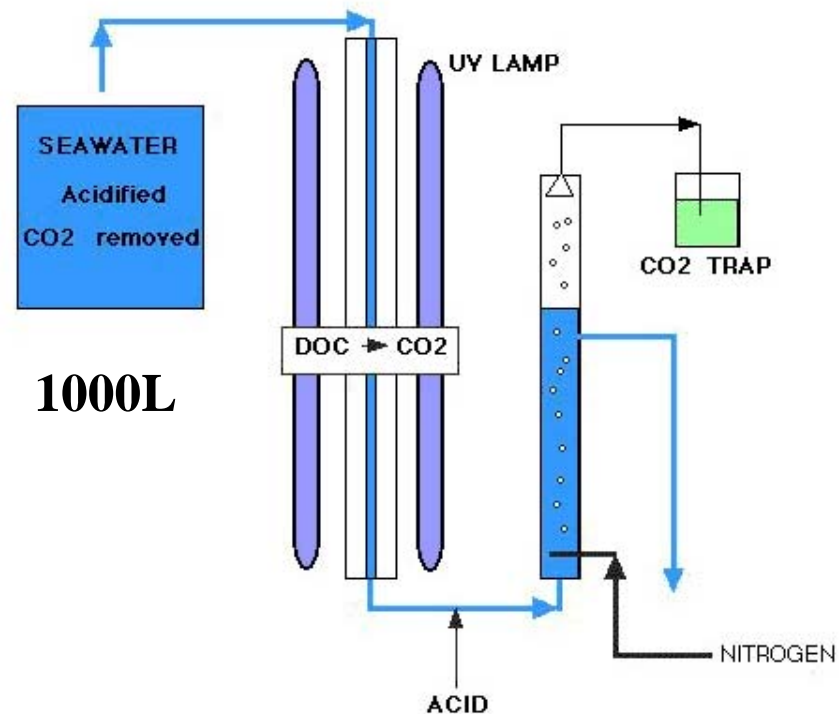
Williams, Oeschger, and Kinney; Nature v224 (1969)

## UV photooxidation

### Natural Radiocarbon Activity of the Dissolved Organic Carbon in the North-east Pacific Ocean

THE "age" of the dissolved organic matter in the deep sea relative to its origin in the euphotic zone has been a matter of conjecture for some time<sup>1-3</sup>. Photosynthetic fixation of carbon dioxide into plant carbon by phytoplankton and subsequent biochemical oxidation or solubilization of organic carbon takes place primarily in the upper 0-300 m of the sea. A small, as yet unknown, fraction of this organic carbon is transferred into the deep water by physical processes such as turbulent mixing and sinking of surface water at high latitudes. In addition, particulate organic carbon which sinks from the surface may be converted into dissolved organic matter at depth. In order to determine how "old" this dissolved organic carbon is, its natural radiocarbon activity has been measured for two deep-water samples taken off southern California.

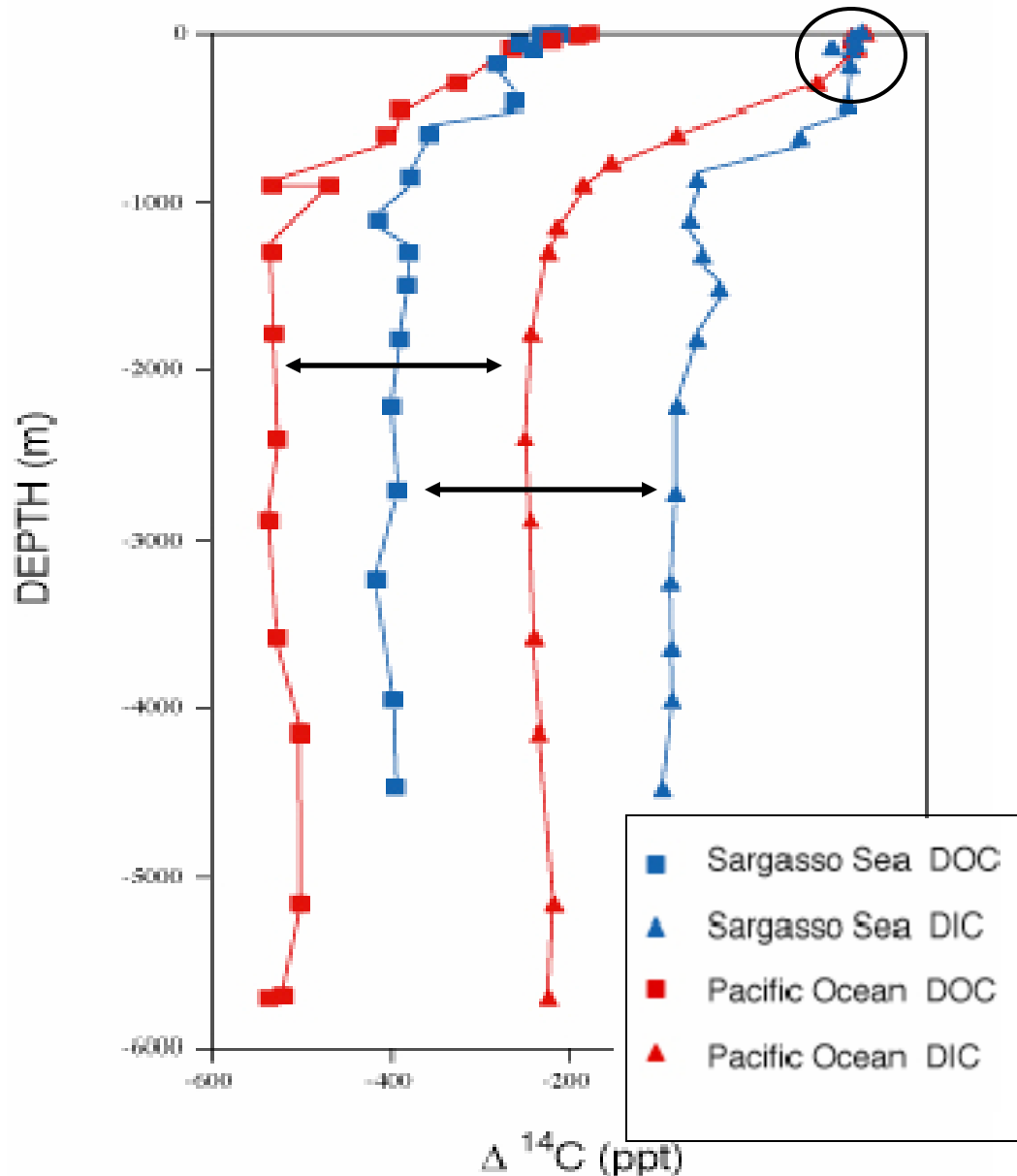
The dissolved organic carbon was converted to carbon dioxide (and subsequently to methane for radiocarbon counting) by photo-oxidation with high energy ultraviolet radiation<sup>4</sup> (Fig. 1). Seawater was collected with a 100 l. stainless steel sampler and stored in 200 l. pre-leached steel drums lined with polythene (no increase in organic carbon was detected during the storage period before analysis). Pre-filtration to remove particulate organic matter was not necessary because its concentration was less than 5 µg/l. The seawater was acidified to pH 2 with hydrochloric acid, sparged free of inorganic carbon (99-97 per cent) with oxygen gas and irradiated in 60 l. batches for 20 h. using a 1,200 W mercury-arc lamp (Hanovia Engelhardt '189 A'). The carbon dioxide so formed was sparged from the seawater with oxygen gas and trapped in strontium hydroxide as strontium carbonate. Complete oxidation was ascertained by comparison of the carbon dioxide in the irradiated seawater (detected by a Beckman model 15 infrared analyser) with the amount of carbon dioxide resulting from the wet combustion of the organic carbon in the seawater before oxidation<sup>5,6</sup>. The strontium carbonate was collected by filtration, washed with water in a nitrogen atmosphere and then dried *in vacuo*.



Depth	$\Delta^{14}\text{C}(\text{‰})$	Age
1880m	-351 ‰	-3470 $\pm$ 330 ybp
1920m	-341 ‰	-3350 $\pm$ 300 ybp

# Radiocarbon in the Atlantic and Pacific Oceans

Peter M. Williams and Ellen Druffel; Nature 1987, JGR 1992



DIC  $^{14}\text{C}$  in surface waters of the Atlantic and Pacific has the same isotopic value.

DOC is always older than DIC (by 4 kyrs in surface water)

Deep ocean values of DOC are equal to a radiocarbon age of 4000-5000 yrs

Either there is a source of "old" DOC, or DOC persists for several ocean mixing cycles